

The Ant Genus *Tetraponera* in the Afrotropical region: the *T. grandidieri* group (Hymenoptera: Formicidae)

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Abstract.—Ants in the *Tetraponera grandidieri* group are endemic to the island of Madagascar, where they occur in relatively undisturbed mesic forest. In this taxonomic revision of the group seven species are recognized: *T. grandidieri* (Forel), *T. hespera* sp. n., *T. hirsuta* sp. n., *T. inermis* sp. n., *T. manangotra* sp. n., *T. merita* sp. n. and *T. variegata* (Forel) stat. n. *T. grandidieri hildebrandti* (Forel) is proposed as a new synonym of *T. grandidieri*. The species in this group show limited morphological and genetic divergence. The justification for treating them as different species is that they occur sympatrically in various combinations, without showing genetic or phenotypic intergradation. Although differences in shape, pilosity and sculpture are not pronounced, there is notable color pattern variation, both within and among species. The conspicuous orange and reddish-brown color that characterizes the workers and queens likely serves as warning coloration. These ants have painful stings and several species of ants in the *Camponotus putatus* complex exhibit color patterns that apparently mimic those of the *T. grandidieri* group.

Twig-dwelling ants in the subfamily Pseudomyrmecinae are a distinctive component of the arboreal ant fauna in forests and woodlands of both the Neotropics and Paleotropics (Ward and Downie 2005). The Afrotropical representatives of the subfamily, currently placed in the genus *Tetraponera* F. Smith, were recently divided into five monophyletic species groups (Ward 2006). Four of the five groups occur in Madagascar and one of these, the *Tetraponera grandidieri* group, is endemic to the island. The group has never received the benefit of a modern taxonomic treatment. There is only a single named species, *T. grandidieri* (Forel), with two nominal subspecies, but the current study reveals substantially greater species-level diversity, paralleling the situation for the ant fauna of Madagascar as a whole, where considerable numbers of species remain undescribed (Fisher 2003). Species are here delimited using a combination of morphological, geographical and genetic evidence, while working within the framework of the

biological species concept (Mayr 1963; Coyne and Orr 2004).

This paper is dedicated to the memory of Roy Snelling, a colleague, friend and ardent hymenopterist. In his later years Roy developed an interest in the ant fauna of the Afrotropical region, specifically that of Kenya, and his last days were spent there. Roy's generosity, candor, pungent humor, and enthusiasm for ants and other aculeate Hymenoptera left an indelible impression on those who had the pleasure of interacting with him.

MATERIALS AND METHODS

Specimens were examined in the following collections:

BMNH	Natural History Museum, London, UK
CASC	California Academy of Sciences, San Francisco, CA, USA
CUIC	Cornell University Insect Collection, Ithaca, NY, USA
MCSN	Museo Civico de Historia Natural "Giacomo Doria", Genoa, Italy

MCZC	Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA	FW	Maximum width of profemur, measured in the same view as FL and at right angles to it.
MHNG	Muséum d'Histoire Naturelle, Geneva, Switzerland	PL	Length of the petiole in lateral view from the lateral flanges of the anterior peduncle to the posterior margin of the petiole.
MNHN	Muséum National d'Histoire Naturelle, Paris, France	PH	Maximum height of petiole, measured in the same view as PL, and excluding protruding teeth or lobes at the anteroventral or posteroventral extremities of the petiole.
NHMB	Naturhistorisches Museum, Basel, Switzerland	DPW	Maximum width of petiole, measured in dorsal view.
NHNV	Naturhistorisches Museum, Vienna, Austria	LHT	Length of the metatibia, excluding the proximomedial condyle (Ward 2001, fig. 5).
PSWC	P. S. Ward Collection, University of California at Davis, CA, USA	CI	Cephalic index: HW/HL
SAMC	South African Museum, Cape Town, South Africa	FCI	Frontal carina index: MFC/HW
UCDC	Bohart Museum of Entomology, University of California at Davis, CA, USA	REL	Relative eye length: EL/HL
USNM	National Museum of Natural History, Washington, DC, USA	REL2	Relative eye length, using HW: EL/HW

Standard measurements (in mm) and setal counts were taken at 50× with a Wild M5A microscope, as described in Ward (2001, 2006). The abbreviations used for measurements, indices and setal counts are given below. The first four measurements are taken with the head in full-face view, such that the posterior margin of the head and the anterolateral corners are in the same plane of view.

HW	Maximum head width, including eyes.	SI	Scape index: SL/HW
HL	Head length, taken along the midline, from the posterior margin of the head to the anterior extremity of the clypeus.	FI	Profemur index: FW/FL
EL	Eye length, measured in the same plane of view as HL.	PLI	Petiole length index: PH/PL
MFC	Minimum distance between the frontal carinae.	PWI	Petiole width index: DPW/PL
SL	Scape length, excluding the radicle.	CSC	Cepalic setal count: number of standing hairs (those forming an angle of 45° or more with the cuticular surface) visible on the posterior half of the head, as seen in lateral and posterior views
FL	Length of profemur, measured along its long axis in posterior view.	MSC	Mesosomal setal count: number of standing hairs visible in profile (lateral view) on the mesosoma dorsum

Automontage images of selected specimens (Figs 7–22) were taken by April Nobile and Erin Prado at the California Academy of Sciences (CAS), under the direction of Brian Fisher. These images are also posted on AntWeb (www.antweb.org), together with photographs of the type specimens of *T. grandidieri*, *T. grandidieri hildebrandti* (Forel) and *T. grandidieri variegata* (Forel).

The species described here were sequenced for fragments of one mitochondrial gene (COI) and several nuclear genes, using methods described in Ward and Downie (2005) and Brady et al. (2006). This molecular work is ongoing and results will be analyzed and presented in more detail elsewhere. The DNA sequence data provide ancillary information that helps to validate species boundaries inferred from morphology and geography.

Species distributions were plotted with the shareware program Versamap (Version 3.01). For most specimens examined in this study the coordinates (latitude and longitude) were given on the specimen label. For material lacking this information the following sources were used to georeference collection sites: Forel (1892), United States Board on Geographic Names (1989), Viette (1991), Huber (2003), the GEONet Names Server (<http://earth-info.nga.mil/gns/html/index.html>), the Gazetteer to Malagasy Botanical Collecting Localities (<http://www.mobot.org/MOBOT/Research/madagascar/gazetteer/>), and topographic maps of Madagascar at scales of 1:50,000, 1:100,000 and 1:500,000, published by Foiben-Taosarintanin' i Madagasikara (Institut Géographique et Hydrographique National). In the lists of material examined, most locality names are given verbatim from the specimen label, but in a few instances they have been interpreted for clarity. In this case the original spelling is given in quotes after the emendation (e.g., Anosibe An'ala [as "Nosibé, Village de l'Imerina"]). The abbreviation "c.u." signifies collector unknown.

RESULTS

Diagnosis of the *Tetraoponera grandidieri* group

(modified from Ward 2006)

Worker diagnosis. Medium to large species (HW 0.95–1.59, HL 1.05–2.01, LHT 1.05–1.83); masticatory margin of mandible

with four teeth; basal margin with 0–1 teeth and subequal in length to masticatory margin; labrum with a pair of tubercles closely flanking the midline near the proximal margin but lacking a median tubercle; palp formula 6,4; anteromedial margin of clypeus crenulate or emarginate; distance between frontal carinae exceeding basal scape width (FCI 0.11–0.18), scape length three-quarters or more of head width (SI 0.72–0.83); eye length about one-third of head length (REL 0.28–0.36); head capsule with three distinct ocelli; pronotum laterally marginate, but not strongly so; mesopropodeal impression well developed (Figs 5, 6); petiole relatively long (PLI 0.49–0.59, PWI 0.40–0.65); posteroventral margin of petiole lying adjacent to helcium venter; metabasitarsal sulcus present; legs long and slender (FI 0.28–0.36, LHT/HL 0.85–1.12); appressed pubescence sparse on abdominal tergite 4; standing pilosity uncommon (CSC 2-3, MSC 1-6), absent from mesonotum, propodeum, and extensor surfaces of the tibiae. Orange to reddish-brown, head concolorous or darker; gaster and portions of femora may also be infuscated.

Comments. Distinctive features of the worker caste of the *T. grandidieri* group include the relatively large body size, long legs and antennal scapes, presence of three ocelli, deeply impressed mesopropodeal impression, and conspicuous orange to reddish-brown body coloration. Other Malagasy *Tetraoponera* species have shorter scapes and legs (SI 0.40–0.70, LHT/HL 0.58–0.82), 0–2 ocelli on the head, a shallower mesopropodeal impression, and usually darker body color. Additional differences between the *T. grandidieri* group and the other four species groups of Afrotropical *Tetraoponera* are given in Ward (2006).

Synonymic list of species

T. grandidieri (Forel 1891: 203)
= *T. grandidieri hildebrandti* (Forel 1891: 203)
syn. n.

T. hespera sp. n.
T. hirsuta sp. n.
T. inermis sp. n.

T. manangotra sp. n.
T. merita sp. n.
T. variegata (Forel 1895: 487) stat. n.

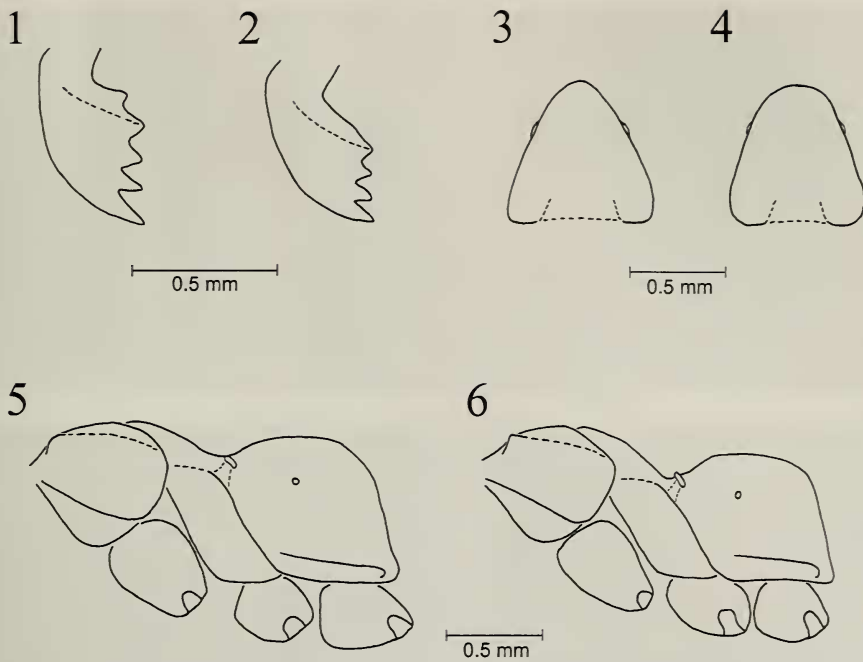
KEY TO SPECIES BASED ON THE WORKER CASTE

- 1 Basal margin of mandible with a prominent tooth, in addition to four teeth on the masticatory margin (Fig. 1); anterior clypeal margin deflected ventrally; widespread in eastern and northern Madagascar *merita*
- Basal margin of mandible lacking tooth, masticatory margin with four teeth (Fig. 2); anterior clypeal margin directed forward, not deflected ventrally 2
- 2(1) Petiole broad (PWI 0.61–0.65, DPW/HW 0.50–0.53), subtriangular in dorsal view, and with a relatively short, thick anterior peduncle (Fig. 20); larger species, HW 1.48–1.58, LHT 1.64–1.76; known only from extreme southern Madagascar *manangotra*
- Petiole more slender (PWI 0.40–0.53, DPW/HW 0.30–0.40), obovate, and with a thin, elongate anterior peduncle (e.g., Figs 14, 16, 18); smaller species, HW 0.95–1.44, LHT 1.05–1.59; widespread 3
- 3(2) Scape with conspicuous suberect and subdecumbent hairs (Fig. 13); body tricolored: metasoma, appendages, and ventral margin of mesosoma orange, most of mesosoma reddish-brown, and head dark brownish black; endemic to Manongarivo Massif *hirsuta*
- Most hairs on scape appressed or decumbent, and generally inconspicuous, except those at the apex (e.g., Fig. 9); body color variable but usually without preceding tricolor pattern 4
- 4(3) Metanotal spiracle not protruding above the profile of the mesosoma, as seen in lateral view (Fig. 5); head broad (CI 0.88–0.97); head and mesosoma reddish-brown, metasoma and appendages paler; widespread in eastern Madagascar *inermis*
- Metanotal spiracle more or less protruding above the profile of the mesosoma, as seen in lateral view (Fig. 6); head usually more elongate (CI 0.77–0.90); color variable 5
- 5(4) Dorsum of propodeum laterally compressed, the propodeum appearing subtriangular in posterior view (Fig. 3); body concolorous orange-brown; northern Madagascar *hespera*, in part (Ankarana population)
- Dorsum of propodeum more broadly rounded, the propodeum appearing dome-shaped in posterior view (Fig. 4); color variable 6
- 6(5) Legs uniformly light orange-brown, femora lacking conspicuous black banding; body usually bicolored, such that dark head contrasts with lighter orange-brown mesosoma and metasoma (Fig. 8), less commonly unicolorous orange; widespread and variable species *grandidieri*
- Legs light orange-brown, with contrasting black bands on the distal portions of the mesofemur and metafemur (Figs 10, 22); body concolorous or bicolored (in latter case both head and gaster are dark brownish-black) 7
- 7(6) Body concolorous yellow brown or orange brown (Fig. 10); northwestern Madagascar *hespera*, in part (most populations)
- Body bicolored, head and gaster dark brown and contrasting with the lighter mesosoma (Fig. 22); eastern Madagascar *variegata*

Tetraponera grandidieri (Forel 1891)
 (Figs 7–8, 19)

(MCSN, MHNG) [examined] [Two of three MHNG syntypes imaged on AntWeb: CASENT0101652, CASENT0102029]. One syntype (CASENT0101652) here designated lectotype.

Sima Grandidieri Forel 1891: 203. Syntypes, 4 workers, Central Madagascar (Hildebrandt)



Figs 1–6. Workers of the *Tetraponera grandidieri* group, right mandible (1, 2), posterior view of propodeum (3, 4), and lateral view of mesosoma (5, 6). 1, *T. merita*; 2, *T. hespera*; 3, *T. hespera*, Ankarana population; 4, *T. hespera*, Nosy Bé; 5, *T. inermis*; 6, *T. hespera*.

Sima Grandidieri var. *Hildebrandti* Forel 1891: 204. Holotype (by monotypy) worker, Pays de Betsileo, "Sud Central Madagascar" (Hildebrandt) (MHNG) [examined] [Imaged on AntWeb: CASENT0101883]. *Syn. n.*

Sima grandidieri Forel; Forel 1891: 229–230. Description of queen and male.

Tetraponera grandidieri (Forel); Wheeler 1922: 1014. Combination in *Tetraponera*.

Tetraponera grandidieri var. *hildebrandti* (Forel); Wheeler 1922: 1014. Combination in *Tetraponera*.

Tetraponera grandidieri (Forel); Ward, 1991: 342. Nesting biology.

Tetraponera grandidieri (Forel); Fisher 1996: 100; Fisher 1999: 134; Fisher 2002: 318. Cited in faunal inventories.

Tetraponera cf. *grandidieri* (Forel); Fisher 1998: 49. Cited in faunal inventory.

Tetraponera grandidieri (Forel); Ward and Downie 2005. DNA sequences of five nuclear genes; GenBank accession numbers AY703507 (18S rDNA), AY703574 (28S rDNA), AY703641 (wingless), AY703775 (long wavelength rhodopsin), and AY703778 (abdominal-A).

Material Examined.—(BMNH, CASC, MCSN, MCZC, MHNG, MNHN, NHMB, NHMV, PSWC, SAMC, UCDC, USNM) MADAGASCAR *Antananarivo*: Andrangoloaka (Sikora); *Antsiranana*: Montagne d'Ambre [?] [as "Amber geb."'] (Rolle); 1 km W Andampibe, Cap Masoala, 125 m (Alpert, G. D.); 3 km W Andampibe, Cap Masoala, 125 m (Alpert, G. D.); 3 km W Sakalava Beach, 40 m (Schlinger; et al.); 4 km SW Ambohitra (=Joffreville), 1000 m (Ward, P. S.); 5 km SW Ambohitra (=Joffreville), 1100 m (Ward, P. S.); 7 km N Joffreville, 360 m (Harin'Hala, R.); Betaolana forest, 880 m (Fisher, B. L.; et al.); Diego Suarez (Alluaud, C.); Forêt Ambanitaza, 26.1 km 347° [NNW] Antalaha, 240 m (Fisher, B. L.; et al.); Forêt Binara, 9.1 km 233° SW Dairana, 650–800 m (Fisher, B. L.; et al.); Forêt Binara, 9.4 km 235° SW Dairana, 1100 m (Fisher, B. L.; et al.); Fotodriana, Cap Masoala, 25 m (Alpert, G. D.; et al.); Fotodriana, Cap Masoala, 25 m (Alpert, G. D.); Marojejy R.N.I., #12, 375 m (Alpert, G. D.); Marojejy R.N.I., #12, 665 m (DiRosa, R.); Montagne d'Ambre, 900 m (Alpert, G.; et al.); Montagne d'Ambre, Petit Lac, 1000 m (Alpert, G.; et al.); Montagne Française, 150 m (Harin'Hala, R.); P.N. Marojejy,



Figs 7–12. Automontage images of workers of the *Tetraponera grandidieri* group, full-face (dorsal) view of head (7, 9, 11) and lateral view of body (8, 10, 12). 7, 8, *T. grandidieri* (CASENT0012861); 9, 10, *T. hespera*, holotype (CASENT0012865); 11, 12, *T. hespera*, Ankarana population (CASENT0012864).

26.6 km 31° NE Andapa, 1325 m (Fisher, B. L.; et al.); P.N. Marojejy, 27.6 km 35° NE Andapa, 775 m (Fisher, B. L.; et al.); P.N. Marojejy, 28.0 km 38° NE Andapa, 450 m (Fisher, B. L.; et al.); P.N. Montagne Ambre, 1125 m (Harin'Hala, R.); P.N. Montagne Ambre, 3.6 km 235° SW Joffreville, 925 m (Fisher, B. L.; et al.); P.N. Montagne

Ambre, 960 m (Harin'Hala, R.); P.N. Montagne Ambre, 960 m (Irwin, M. E.; et al.); P.N. Montagne Ambre, 960 m (Schlinger; et al.); P.N. Montagne Ambre, 975 m (Irwin, M. E.; et al.); Parc Nat. Mont. d'Ambre [as "Amber Mt. Nat. Pk."], 3000 ft. (Alpert, G. D.); Parc Nat. Mont. d'Ambre [as "Amber Mt. Nat. Pk."], 3200



Figs 13–18. Automontage images of workers of the *Tetraoponera grandidieri* group, full-face (dorsal) view of head (13, 15, 17) and lateral view of body (14, 16, 18). 13, 14, *T. hirsuta*, holotype (CASENT0170370); 15, 16, *T. inermis*, holotype (CASENT0012862); 17, 18, *T. merita*, holotype (CASENT0012863).

ft. (Alpert, G. D.); Parc Nat. Mont. d'Ambre [as "Amber Mt. Nat. Pk."], 3600 ft. (Alpert, G. D.); Parc Nat. Mont. d'Ambre, 1000–1100 m (Brown, W. L.; Brown, D. E.); Parc Nat. Montagne d'Ambre, 1100 m (Olson, D. M.); R.S. Manongarivo, 10.8 km 229° SW Antanambao, 400 m (Fisher, B. L.); R.S. Manongarivo, 12.8 km 228°

SW Antanambao, 780 m (Fisher, B. L.); R.S. Manongarivo, 14.5 km 220° SW Antanambao, 1175 m (Fisher, B. L.); Réserve Spéciale Ambre, 3.5 km 235° SW Sakaramy, 325 m (Fisher, B. L.; et al.); Sakalava Beach, 10 m (Harin'Hala, R.); Fianarantsoa: 3 km W Ranomafana, nr. Ifanadiana, 950 m (Ward, P. S.); 40 km S Ambalavao,



Figs 19–22. Automontage images of workers of the *Tetraponera grandidieri* group, full-face (dorsal) view of head (19, 21) and lateral view of body (20, 22). 19, 20, *T. manangotra*, paratype (CASENT0121948); 21, 22, *T. variegata* (CASENT0409559).

Rés. Andringitra, 1275 m (Fisher, B. L.); 45 km S Ambalavao, 720 m (Fisher, B. L.); 7 km W Ranomafana Natl. Park, 1000 m (Steiner, K.); 7 km W Ranomafana Natl. Park, 1000 m (Steiner, W. E.; Zack, S.); 7 km W Ranomafana, 1000 m (Stebbins, M.; et al.); 7 km W Ranomafana, 900 m (Steiner, W. E.); 8 km E Kianjavato, 145 m (Alpert, G.); 9 km ESE Ranomafana, nr. Ifanadiana, 600 m (Ward, P. S.); FC Vatovavy, 175 m (Fisher, B. L.; et al.); Ivohibe, 1500 m (Decary, R.); Maharira Forest, Ranomafana Natl Pk, 1350 m (Rajeriarison, E.); Maharira Forest, Ranomafana Natl Pk, 1375 m (Rajeriarison, E.); Miaranony, Ranomafana Natl Pk, 1050 m (Rajeriarison, E.); Miaranony, Ranomafana Natl Pk, 700 m (Rajeriarison, E.); Pays de Betsileo, "Sud Central Madagascar" (Hildebrandt); P.N. Ranomafana, 0.4 km WSW park entrance, 900 m (Kavanaugh, D. H.; Kavanaugh, K. M.); P.N. Ranomafana, 1020 m (Harin'Hala, R.); P.N. Ranomafana, 1130 m (Harin'Hala, R.); P.N.

Ranomafana, Vatoharanana, 4.1 km 231° SW Ranomafana, 1100 m (Fisher, B. L.; et al.); P.N. Ranomafana, Vohiparara, 1110 m (Harin'Hala, R.); PN Befotaka-Midongy, 940 m (Fisher, B. L.; et al.); R.S. Ivohibe, 8.0 km E Ivohibe, 1200 m (Fisher, B. L.); Ranomafana (Pauly, A.); Ranomafana N. P., 1000 m (Alpert, G.; et al.); Ranomafana N.P., Talatakely Forest, Piste S 100, 900 m (Rajeriarison, E.); Ranomafana N.P., Vohiparara Forest, 1200 m (Rajeriarison, E.); Ranomafana National Park, Talatakely, 915–1000 m (Lee, V. F.; Ribrado, K. J.); Ranomafana Natl Pk. (Rajeriarison, E.); Ranomafana Natl Pk., 950–1100 m (Bartolozzi, L.; et al.); Ranomafana Natl. Pk., Saharoemba ZP, 800 m (Rabeson, P.); Ranomafana NP, Talatakely (Griswold, C. E.; Ubick, D.); Ranomafana, Ambatolahy forest (Rajeriarison, E.); Ranomafana, Ambatovory forest, 1035 m (Rajeriarison, E.); Ranomafana, Miaranony Village (Kingman, A.); Ranomafana, Vohiparara forest, 1160 m (Rajeriarison, E.);

Vevembe, 600 m (Fisher, B. L.; et al.); *Toamasina*: 10 km S Cap Este, 5 km W, 20 m (Alpert, G. D.); 14 km W Cap Est, Ambato, 100 m (Alpert, G. D.); 17 km W Andapa, Rés. d'Anjanaharibe-Sud, 875 m (Alpert, G. D.); 19 km ESE Maroantsetra, 250 m (Ward, P. S.); 19 km ESE Maroantsetra, 300 m (Ward, P. S.); 19 km ESE Maroantsetra, 350 m (Ward, P. S.); 1 km SSW Andasibe (=Périnet), 920 m (Ward, P. S.); 6.3 km S Ambanizana, Andranobe, 25 m (Fisher, B. L.); 6.5 km SSW Befingotra, Res. Anjanaharibe-Sud, 875 m (Fisher, B. L.); 6.9 km NE Ambanizana, 1080 m (Fisher, B. L.); 6.9 km NE Ambanizana, 650 m (Fisher, B. L.); 8 km ESE Andasibe (=Périnet), 800 m (Ward, P. S.); Ambodiriana, 125 m (Fisher, B. L.; et al.); Ampasimbe, 450 m (Betsch, J.-M.); Andasibe (Périnet) (Brooks, R. W.); Andasibe PN, 1025 m (Harin'Hala, R.); Anosibe An'ala [as "Nosibé, Village de l'Imerina"] (Sikora); Antongil (Mocquerys); Asanoroeyo, 3 km W Anosibe An'ala (Raharimina, C.); Baie d'Antongil (c.u.); Betampona, 520 m (Fisher, B. L.; et al.); Kalalao, 100 m (Fisher, B. L.; et al.); Manakambahiny (Pauly, A.); Mont. Akirindro, 7.6 km 341° NNW Ambinanitelo, 600 m (Fisher, B. L.; et al.); Mont. Anjanaharibe, 18.0 km 21° NNE Ambinanitelo, 470 m (Fisher, B. L.; et al.); Mont. Anjanaharibe, 19.5 km 27° NNE Ambinanitelo, 1100 m (Fisher, B. L.; et al.); Nosey Mangabe (Alpert, G. D.); Nosey Mangabe, <5 m (Ward, P. S.); Nosey Mangabe, 150 m (Ward, P. S.); Nosey Mangabe, 20 m (Ward, P. S.); Nosey Mangabe, 300 m (Ward, P. S.); Nosey Mangabe, 3 m (Fisher, B. L.; et al.); P.N. Mantadia, 895 m (Ratsirarson, H. J.); Périnet (Noyes, J. S.; Day, M. C.); Périnet (Ross, E. S.); PN Mananara-Nord, 225 m (Fisher, B. L.; et al.); PN Zahamena, 860 m (Fisher, B. L.; et al.); PN Zahamena, Besaky River, 760 m (Fisher, B. L.; et al.); PN Zahamena, Oribe River, 780 m (Fisher, B. L.; et al.); PN Zahamena, Sahavorondrano River, 765 m (Fisher, B. L.; et al.); Saint Marie, Forêt de Kalalao (Madl); St. Marie (c.u.); Tampolo, 218 m (Fisher, B. L.; et al.); *Toliara*: 10 km NW Enakara, Rés. Andohahela, 420 m (Fisher, B. L.); 10 km NW Enakara, Rés. Andohahela, 430 m (Fisher, B. L.); 10 km SSW Eminiminy, 750 m (Rajeriarison, E.); 11 km NW Enakara, Rés. Andohahela, 800 m (Fisher, B. L.); 5 km NNW Isaka-Ivondro, Rés. Andohahela, 280 m (Ward, P. S.); 5 km WNW Mandiso, Rés. Andohahela, 400 m (Ward, P. S.); Col de Manangotry, c.30 km N Fort Dauphin, ~1000

m (Whitacre, D.); Forêt Ivohibe, 650 m (Fisher, B. L.; et al.); Fort Dauphin (Alluaud, C.); Manatantely, 100 m (Fisher, B. L.; et al.); P.N. Andohahela, 3.8 km 113° ESE Mahamavo, 900 m (Fisher, B. L.; et al.); P.N. Andohahela, Manampanihy, 5.4 km 113° ESE Mahamavo, 650 m (Fisher, B. L.; et al.); PN Andohahela, 275 m (Fisher, B. L.; et al.); Rés. Andohahela, Marosohy, 600 m (Fisher, B. L.); Vallee d'Ambolo, Col de Sakalavana (Alluaud, C.); *province unknown*: "Central Madagascar" (Hildebrandt); "Centre de Madag" (Hildebrandt); "Madag." (Sikora); "Madagascar Centralis" (Hildebrandt); "Madagascar" (c.u.); "Madagascar" (de Gaulle, J.); "Madagascar" (Grandidier); "Madagascar" (Sikora); "Madagascar/(S.-E.)" (Decary, R.).

Worker measurements (n = 13). HW 1.01–1.44, HL 1.20–1.65, LHT 1.07–1.56, CI 0.77–0.88, FCI 0.15–0.17, REL 0.28–0.36, REL2 0.34–0.43, SI 0.74–0.81, FI 0.29–0.36, PLI 0.50–0.59, PWI 0.40–0.53.

Worker diagnosis. With characteristics of the *T. grandidieri* group (see above); basal margin of mandible edentate; anterior clypeal margin broadly convex and crenulate, directed forward, not anteroventrally; head relatively elongate (CI 0.77–0.88); metanotal spiracle more or less visible in lateral view of mesosoma, protruding dorsally in the mesopropodeal impression; dorsal face of propodeum broadly convex in lateral and posterior views; standing pilosity generally sparse; long paired setae (0.2–0.4 mm in length) distributed as follows: 1 pair between the frontal carinae, 1 pair on upper half of head, 1 pair on the pronotum, 0–2 pairs on the petiole; 1–2 pairs on the postpetiole; standing pilosity scattered on successive abdominal segments (gastric segments 1–4); short appressed to subdecumbent hairs absent or inconspicuous on most of body; integument mostly sublucid, with fine coriarioid/punctulate sculpture; body orange-brown, appendages lighter; head usually dark brown to brownish-black, but concolorous with rest of body in some northern populations (see discussion below); legs uniformly light orange-brown.

Comments. This species is typically bicolored with a black or dark brown head and the remainder of the body a contrasting orange-brown. This allows it to be distinguished from the other two species, *T. inermis* and *T. merita*, with which it is widely sympatric—both of these usually have the head more or less concolorous with the mesosoma. Some northern populations of *T. grandidieri* have workers that are unicolorous orange-brown, however, and these superficially resemble the other two species. They can be recognized because they lack a tooth on the basal margin of the mandible (present in *T. merita*) and the metanotal spiracle protrudes from the mesosoma dorsum in profile (not protruding in *T. inermis*). The degree of prominence of the metanotal spiracle varies, however, so it is also useful to examine head shape, which is more elongate in *T. grandidieri* (worker CI 0.77–0.88 versus 0.88–0.97 in *T. inermis*; see also additional discussion under *T. inermis*). *T. grandidieri* also overlaps in distribution with *T. hespera* in northern Madagascar. Where these two species co-occur *T. grandidieri* has a bicolored body, while *T. hespera* has a unicolorous body and contrasting dark bands on the femora.

At Betampona (17°53'S 49°12'E) Brian Fisher collected three nest series of *T. grandidieri*: one (BLF13292) with unicolorous workers, a second (BLF13298) with bicolored workers, and a third (BLF13349) with both unicolorous and bicolored workers, in approximately equal proportions. The Betampona workers with light and dark heads show no obvious differences other than color. The occurrence of both forms in the same nest is consistent with the view that they are conspecific. In addition, genetic data (>10 kb of sequence data from several nuclear genes and one mitochondrial gene) from populations sampled throughout the range of the species show the two color forms to be phylogenetically comingled (Ward unpubl.).

Both color forms are here treated as conspecific but further studies are needed to clarify their status. It is possible that these color morphs show some degree of reproductive isolation and/or ecotypic differentiation. As indicated below, they appear to be involved in a mimicry complex with some species of *Camponotus*.

Finally it should be noted that there are nine specimens of *T. grandidieri* in the Forel collection in MHNG (Geneva) labeled as "Typus" or "Cotypus" but most are not true types, because the label data exclude this possibility. These non-types include three males (from Andrangoloaka), one dealate queen (from Andrangoloaka) and one worker (from "Nosibé, Village de l'Imerina"), all with a red "Typus" label, and an alate queen (Madagascar/Sikora) labeled "Cotypus". Only three workers in MHNG are apparently part of the actual type series of *T. grandidieri* (there is also a syntype worker in MCSN). To avoid confusion I have designated one of the MHNG syntype workers as lectotype.

Distribution and biology. *Tetraponera grandidieri* is widespread in eastern Madagascar, with a distribution that spans the length of the island (Fig. 23). Populations are restricted to rainforest, at elevations ranging from sea level to 1375 m. As a result of habitat destruction in the lowlands most populations are found at intermediate or higher elevations. Colonies usually occupy dead twigs or branches on the ground, less commonly in the lower canopy. During field work in Madagascar I collected thirteen nest series of this species, of which nine were in dead wood and four were located in cavities of live plants: three in stems of tree saplings (*Ixora* sp., *Leea* sp. and an unidentified plant), and one in a cavity in a live root of a tree in the genus *Rhus*. There were no scale insects (Coccoidea) in any of these live cavity nests, however, and there is no indication that *T. grandidieri* is closely associated with any particular plant species. It seems clear that it and other members of the *T. grandidieri*

group occupy moister nest sites than most *Tetraponera* species. The nests of *T. grandidieri* apparently contain no more than one dealate queen, and colony sizes are small (5–40 workers). Alate queens and males have been collected from February to May. Workers commonly forage on low vegetation, and they appear to be mimicked by members of the *Camponotus putatus* complex whose workers forage in similar microhabitats. *T. grandidieri* is generally absent from disturbed rainforest edge and other high light environments.

Tetraponera hespera sp. n.
(Figs 2–4, 6, 9–12, 24)

Tetraponera psw110; Fisher 2002: 318. Cited in faunal inventory.

Holotype worker. MADAGASCAR Antsiranana: Nosy Be, 4 km ESE Andoany (=Hellville), 100 m, 13°25'S 48°18'E, 2.v.1989, ex rotten stick on ground, rainforest, P. S. Ward#10457 (CASENT0012865) (CASC).

Paratypes. Series of workers and queens, same locality and date as holotype, elevation 100–200 m (P. S. Ward#10456, 10457, 10459, 10463, 10465, 10470-1) (BMNH, CASC, MCZC, PSWC, SAMC, UCDC).

Material Examined.—(BMNH, CASC, MCZC, PSWC, SAMC, UCDC) MADAGASCAR *Antsiranana*: Ampasindava, Ambilanivy, 3.9 km 181° S Ambaliha, 600 m (Fisher, B. L.; et al.); Forêt Antsahabe, 11.4 km 275° W Dairana, 550 m (Fisher, B. L.; et al.); Forêt Binara, 9.1 km 233° SW Dairana, 650–800 m (Fisher, B. L.); Nosy Be, 4 km ESE Andoany (=Hellville), 100 m (Ward, P. S.); Rés. Ankarana, 7 km SE Matsaborimanga, 150 m (Ward, P. S.); Rés. Spéc. Ankarana, 13.6 km 192° SSW Anivorano Nord, 210 m (Alpert, G. D.; et al.); Rés. Spéc. Ankarana, 13.6 km 192° SSW Anivorano Nord, 210 m (Fisher, B. L.; et al.); Rés. Spéc. Ankarana, 22.9 km 224° SW Anivorano Nord, 80 m (Fisher, B. L.; et al.); R.S. Manongarivo, 10.8 km 229° SW Antanambao, 400 m (Fisher, B. L.); R.S. Manongarivo, 12.8 km 228° SW Antanambao, 780 m (Fisher, B. L.); *Toliara*: Ambohijanahary, 34.6 km 314° NW Ambaravarana,

1100 m (Fisher, B. L.; et al.); Ambohijanahary, 35.2 km 312° NW Ambaravarana, 1050 m (Fisher, B. L.; et al.).

Worker measurements (n = 13). HW 0.95–1.31, HL 1.19–1.55, LHT 1.12–1.53, CI 0.78–0.90, FCI 0.14–0.18, REL 0.30–0.35, REL2 0.35–0.41, SI 0.77–0.83, FI 0.29–0.34, PLI 0.50–0.58, PWI 0.42–0.53.

Worker diagnosis. Similar to *T. grandidieri* (q.v.). Basal margin of mandible lacking tooth; anterior clypeal margin broadly convex and crenulate, directed forward; head relatively elongate (CI 0.78–0.90); metanotal spiracle visible in lateral view of mesosoma (Fig. 6); dorsal face of propodeum usually broadly convex in posterior view, but more dorsally compressed and subtriangular in one population (see below); standing pilosity and appressed pubescence generally sparse; integument mostly sublucid, with fine coriarius/puncticulate sculpture; body unicolorous yellow-brown or orange-brown, legs usually with contrasting black bands on the distal portions of the femora; banding sometimes weakly developed on the profemur, and absent from all legs in one population.

Comments. *T. hespera* represents an assemblage of variably isolated populations in northwestern Madagascar. This species is most readily recognized by its distinctive color pattern: workers are usually a unicolorous yellow-brown or orange-brown, with contrasting black bands on the legs (Fig. 10). In earlier identifications of museum material I employed a code name for this species: *Tetraponera* psw110.

The *hespera*-like population occupying the Ankarana Massif is divergent in several respects: workers lack the characteristic black leg banding (Fig. 12) and they have a dorsally narrowed propodeum that appears more or less triangular in shape when seen in posterior view (Fig. 3), in contrast to the broadly convex propodeum seen in other populations of *T. hespera* (Fig. 4) and in the rest of the *T. grandidieri* group. Although I considered treating the

Ankarana form as a different species, several observations argued against this. (1) It is strictly allopatric to the more typical morph of *T. hespera*, so there is no "test" of species distinctness in sympatry. (2) Samples from tropical dry forest at Forêt Antsahabe, 60 km southeast of Ankarana, have black leg banding but the propodeum tends to be intermediate in shape between the Ankarana morph and more typical *T. hespera*. (3) A worker (BLF10881; CASENT0053718) from another nearby locality, Forêt Binara, has black leg banding and a broadly convex propodeal dorsum—yet it is genetically identical at the mitochondrial COI locus to a worker from Forêt Antsahabe. The COI data indicate that all three populations (Ankarana, Antsahabe and Binara) are closely related and form a clade that is sister to *T. hespera* + *T. hirsuta*, but with combined nuclear gene sequences the three populations do not form a clade; instead, they are paraphyletic with respect to *T. hirsuta*. Thus, recognizing the Ankarana form as a distinct species would require an arbitrary division along a gradient of differentiated allopatric populations.

Distribution and biology. This species is found in northwestern Madagascar, with an isolated population at Ambohijanahary in central western Madagascar (Fig. 24). It occurs sympatrically with *T. grandidieri*, *T. hirsuta* and *T. merita* at one or more localities. Most populations of *T. hespera* are in seasonally dry rainforest, where colonies tend to nest near the ground level, usually in rotten sticks. One colony from the type locality (PSW10456) was nesting in an earthworm cast on the ground. As in *T. grandidieri*, observed colony sizes are small (4–36 workers).

Tetraponera hirsuta sp. n.

(Figs 13–14, 25)

Holotype worker. MADAGASCAR Antsiranana: R.S. Manongarivo, 10.8 km 229° SW Antanambao, 400 m, 13°57.7'S 48°26.0'E,

8.xi.1998, ex sifted litter, rainforest, B. L. Fisher#1996 (CASENT0170370) (CASC).

Paratypes. 1 worker, 1 dealate queen, same locality and date as holotype, ex rotting tree stump, rainforest (B. L. Fisher#2008; CASENT0170371); 1 worker, MADAGASCAR Antsiranana: R.S. Manongarivo, 12.8 km 228° SW Antanambao, 780 m, 11.xi.1998, ex sifted litter, rainforest (B. L. Fisher#1862; CASENT0170368) (CASC); 2 workers, MADAGASCAR Antsiranana: R.S. Manongarivo, 12.8 km 228° SW Antanambao, 780 m, 12.xi.1998, beating low vegetation, rainforest (B. L. Fisher#1888; CASENT0170369) (CASC).

Material Examined.—Known only from the type material.

Worker measurements (n = 2). HW 1.19–1.34, HL 1.35–1.51, LHT 1.32–1.45, CI 0.88–0.89, FCI 0.15, REL 0.34, REL2 0.39, SI 0.73–0.76, FI 0.33–0.34, PLI 0.57, PWI 0.51–0.53.

Worker diagnosis. Similar to *T. grandidieri* (q.v.). Basal margin of mandible lacking tooth; anterior clypeal margin broadly convex and crenulate, directed forward; metanotal spiracle visible in lateral view of mesosoma; dorsal face of propodeum broadly convex in posterior view; scape with conspicuous suberect and subdecumbent hairs (Fig. 13); standing pilosity and appressed pubescence generally sparse elsewhere, although tending to be better developed than in other species in the *grandidieri* group; integument mostly sublucid, with fine coriarius/puncticulate sculpture; body tricolored: metasoma, appendages, and ventral margin of mesosoma orange, most of mesosoma reddish-brown, and head dark brownish black.

Comments. *T. hirsuta* can be distinguished from related species by the more conspicuous pilosity on the scapes (Fig. 13) and the tricolored body. The differences are slight but consistent, and they are maintained in sympatry with the otherwise similar species *T. grandidieri* and *T. hespera*.

Distribution and biology. This species appears to be endemic to the Manongarivo

Massif (Fig. 25), where it occurs sympatrically with *T. grandidieri*, *T. hespera* and *T. merita*. The only nest series is incomplete: one worker and one dealate queen from a rotting tree stump (BLF2008). Habits are assumed to be similar those of other species in the *T. grandidieri* group, but almost nothing is known about the biology of *T. hirsuta*.

***Tetraponera inermis* sp. n.**
(Figs 5, 15–16, 25)

Tetraponera psw81; Fisher 1996: 100; Fisher 1999: 134. Cited in faunal inventories.

Holotype worker. MADAGASCAR Toamasina: 1 km SSW Andasibe (=Périnet), 920 m, 18°56'S 48°25'E, 16.xi.1990, ex rotten stick on ground, rainforest, P. S. Ward#10941 (CASENT0012862) (CASC).

Paratypes. Series of workers and queens, same locality as holotype, 16.xi.1990 and 12.xii.1990 (P. S. Ward#10940, 19041, 11143) (BMNH, CASC, MCZC, PSWC, SAMC, UCDC).

Material Examined.—(BMNH, CASC, CUIC, MCZC, NHMV, PSWC, SAMC, UCDC) MADAGASCAR *Fianarantsoa*: 43 km S Ambalavao, Res. Andringitra, 825 m (Fisher, B. L.); 8 km E Kianjavato, 145 m (Alpert, G.); FC Vatovavy, 175 m (Fisher, B. L.; et al.); Manombo, 30 m (Fisher, B. L.; et al.); R.S. Ivohibe, 7.5 km ENE Ivohibe, 900 m (Fisher, B. L.); Vevembe, 600 m (Fisher, B. L.; et al.); *Toamasina*: 1 km SSW Andasibe (=Périnet), 920 m (Ward, P. S.); Andasibe (Périnet) (Brooks, R. W.); F.C. Andriantantely, 530 m (Ratsirarson, H. J.); Mont. Anjanaharibe, 18.0 km 21° NNE Ambinanitelo, 470 m (Fisher, B. L.; et al.); Périnet (Noyes, J. S.; Day, M. C.); PN Zahamena, 860 m (Fisher, B. L.; et al.); PN Zahamena, Sahavorondrano River, 765 m (Fisher, B. L.; et al.); Res. Périnet-Analamazotra, 930–1040 m (Olson, D. M.); Res. Périnet-Analamazotra, 950 m (Olson, D. M.); vic. Andasibé (=Périnet), 950–980 m (Brown, W. L.; Brown, D. E.); *Toliara*: 10 km NW Enakara, Rés. Andohahela, 430 m (Fisher, B. L.); 10 km SSW Eminiminy, 750 m (Rajeriarison, E.); 11 km NW Enakara, Rés. Andohahela, 800 m (Fisher, B. L.); 5 km NNW Isaka-Ivondro, Rés. Andohahela, 280 m (Ward, P. S.); 5 km WNW Mandiso,

Res. Andohahela, 400 m (Rajeriarison, E.); 5 km WNW Mandiso, Rés. Andohahela, 400 m (Ward, P. S.); 6 km SSW Eminiminy, 250 m (Alpert, G. D.); 6 km SSW Eminiminy, 250 m (Rabeson, P.); 6 km SSW Eminiminy, 250 m (Rajeriarison, E.); 6 km SSW Eminiminy, Rés. Andohahela, 330 m (Ward, P. S.); 9 km SSW Eminiminy, Rés. Andohahela, 500 m (Ward, P. S.); Forêt Ivohibe, 200 m (Fisher, B. L.; et al.); Fort Dauphin (c.u.); Grand Lavasoa, 450 m (Fisher, B. L.; et al.); P.N. Andohahela, Manampanihy, 5.4 km 113° ESE Mahamavo, 650 m (Fisher, B. L.; et al.); PN Andohahela, 275 m (Fisher, B. L.; et al.).

Worker measurements (n = 11). HW 1.02–1.27, HL 1.05–1.42, LHT 1.05–1.38, CI 0.88–0.97, FCI 0.12–0.15, REL 0.31–0.36, REL2 0.35–0.39, SI 0.72–0.76, FI 0.29–0.31, PLI 0.50–0.55, PWI 0.43–0.53.

Worker diagnosis. Similar to *T. grandidieri* (q.v.). Basal margin of mandible lacking tooth; anterior clypeal margin broadly convex and crenulate, directed forward; head relatively broad (CI 0.88–0.97); metanotal spiracle not visible in lateral view of mesosoma (Fig. 5), subtended laterally and anterolaterally by a pair of concavities that are separated by a transverse carina; dorsal face of propodeum broadly convex in posterior view; standing pilosity and appressed pubescence generally sparse; integument mostly sublucid, with fine coriarius/puncticulate sculpture; head and mesosoma reddish-brown, upper part of propodeum often a darker red than rest of mesosoma; metasoma and appendages paler.

Comments. The worker of this species can be recognized by the absence of a tooth on the basal margin of the mandible; the more or less concolorous reddish-brown body (the upper half of propodeum is often a richer dark red, and the metasoma is paler); and the lack of a protruding metanotal spiracle when the mesosoma is viewed in profile (Fig. 5). In addition, the head tends to be broader than that of *T. grandidieri* and *T. hespera* (CI 0.88–0.97, versus 0.77–0.88 in *T. grandidieri* and 0.78–

0.90 in *T. hespera*). From *T. hespera* it can also be distinguished by the ratio of metatibial length to head width (LHT/HW 1.02–1.09 in *T. inermis*, and 1.10–1.22 in *T. hespera*).

In earlier identifications of museum material I assigned the code name *Tetraoponera* psw81 to this species. During initial examination of *Tetraoponera hirsuta* I misidentified it as *T. inermis*, using the code name *Tetraoponera* psw81. This is the basis for the record of "*Tetraoponera* psw081" from Manongarivo (Fisher 2002: 318). In fact, *T. inermis* is not known from that region.

In the Forel collection (MHNG, Geneva) there is a problematic worker from "Nosibé, village de l'Imerina" [=Anosibe an'Ala at 19°26'S 48°13'E] (leg. Sikora). This worker is large (HW 1.49, LHT 1.79) and unicolored, with an elongate head (CI 0.78), yet the metanotal spiracles are not protruding in lateral view. This individual combines features of *T. inermis* and *T. grandidieri* (unicolored form). At the moment I am unable to identify it with certainty.

Distribution and biology. *T. inermis* occurs in eastern Madagascar from Montagne d'Anjanaharibe to the vicinity of Tolagnaro (Fort Dauphin) (Fig. 25). Collections all come from rainforest, at elevations ranging from 30 m to 1040 m. Nests are located in rotten sticks on the ground, and are small in size. At the type locality I found one dealate queen gleaning the surfaces of leaves, walking rapidly and raising her gaster in the air. She then returned to her nest—a cavity in a small soft dead twig on the ground—which proved to contain eggs, larvae and worker pupae. Thus, this species exhibits non-claustral colony-founding, a trait presumably shared with other members of the *T. grandidieri* group. The gaster-raising behavior was observed in foraging workers of *T. inermis* but not those of the other two species with which *T. inermis* is sympatric: *T. grandidieri* and *T. merita*. *Camponotus reaumuri* Forel (related to *C. putatus* Forel) is a possible mimic of *T. inermis*.

Tetraoponera manangotra sp. n.

(Figs 19–20, 24)

Holotype worker. MADAGASCAR Toliara: PN Andohahela, Manangotry, 33.8 km NW Tolagnaro, 575 m, 24°45.07'S 46°51.47'E, 24.xi.2006, ex dead twig above ground, rainforest, B. L. Fisher#15267 (CASENT0120025) (CASC).

Paratypes. Series of workers and dealate queens, same data as holotype (BMNH, CASC, MCZC, PSWC, SAMC, UCDC); 1 worker, MADAGASCAR Toliara: PN Andohahela, Col de Tanatana, 33.3 km NW Tolagnaro, 275 m, 24°45.52'S 46°51.22'E, 23.xi.2006, beating low vegetation, rainforest, B. L. Fisher#15166 (CASENT0121948) (CASC).

Material Examined.—Known only from the type material.

Worker measurements (n = 4). HW 1.48–1.58, HL 1.77–2.01, LHT 1.64–1.76, CI 0.79–0.83, FCI 0.14–0.16, REL 0.28–0.31, REL2 0.36–0.37, SI 0.77–0.78, FI 0.32–0.33, PLI 0.49–0.55, PWI 0.61–0.65.

Worker diagnosis. Matching the diagnosis of the *T. grandidieri* group (q.v.). Basal margin of mandible lacking tooth; anterior clypeal margin convex, directed forward, and protruding medially; posterior margin of head with low, sharp transverse crest, about 0.30 mm long; metanotal spiracle visible in lateral view of mesosoma; mesopropodeal impression sharply incised; dorsal face of propodeum somewhat flattened, propodeum subquadrate in posterior view; petiole broad and robust, appearing subtriangular in lateral and dorsal views; maximum petiole width about half of head width (DPW/HW 0.50–0.53); anterior peduncle of petiole short and broad; standing pilosity and appressed pubescence similar to that of *T. grandidieri* but with greater number of standing hairs (4–8) on petiole and postpetiole; integument mostly sublucid, with fine coriarius/punctulate sculpture, coarser transverse rugulae on side of mesosoma; body reddish-brown, appendages (except mesofemur and meta-

femur) paler; distal half of flagellum infuscated.

Comments. *T. manangotra* departs somewhat from the general habitus of the *T. grandidieri* group. The protruding median clypeal lobe, strong crest on the posterior margin of the head, and robust petiole are quite distinctive. In dorsal view the petiole is subtriangular in shape and its maximum width is half the head width. In other species in the *T. grandidieri* group the petiole is more slender, not exceeding two-fifths of the head width (DPW/HW 0.30–0.40) and the posterolateral corners of the petiole are broadly rounded. Large size (HW > 1.46, LHT > 1.62) alone separates *T. manangotra* from all other species in the *T. grandidieri* group except *T. merita*. From the latter it can be distinguished by the features mentioned above, as well as the absence of a tooth on the basal margin of the mandible and the more elongate head (CI 0.79–0.83 in *T. manangotra* versus 0.90–0.94 in *T. merita*).

Distribution and biology. This species is known from a single nest series from Col de Manangotry and a foraging worker collected at an adjacent site (Col de Tanatana), in Parc National Andohahela, in rainforest of extreme southern Madagascar. The nest was in a dead twig above the ground, and comprised 5 dealate queens, 47 workers, larvae, prepupae, worker pupae, male pupae and queen pupae. Although the dealate queens were not dissected to evaluate their reproductive state, it seems likely that this species is functionally polygynous. The queens (HW 1.50–1.56, $n = 5$) are about the same size as the workers, whereas in other species in the *T. grandidieri* group (and in most other *Tetraponera*) the queens are notably larger than the workers.

Tetraponera merita sp. n.

(Figs 1, 17–18, 26)

Sima Grandidieri var. *Hildebrandti*; Forel 1892: 260 (in part) (misidentification)

Tetraponera psw92; Fisher 1996: 100; Fisher 1998: 49; Fisher 1999: 134; Fisher 2002: 318. Cited in faunal inventories.

Holotype worker. MADAGASCAR Toamasina: 1 km SSW Andasibe (=Périnet), 920 m, 18°56'S 48°25'E, 16.xi.1990, ex rotting tree stump, rainforest, P. S. Ward#10943 (CASENT0012863) (CASC).

Paratypes. Series of workers and queens, same locality as holotype, 16.xi.1990 and 12.xii.1990 (P. S. Ward#10939, 19043, 10944-3, 11144) (BMNH, CASC, MCZC, PSWC, SAMC, UCDC).

Material Examined.—(BMNH, CASC, MCZC, MHNG, MNHN, NHMV, PSWC, SAMC, UCDC) MADAGASCAR *Antsiranana*: Ampasindava, Ambilanivy, 3.9 km 181° S Ambaliha, 600 m (Fisher, B. L.; et al.); Ampasindava, Ambilanivy, 3.9 km 181° S Ambaliha, 600 m (Rafanomezantsoa, J. J.); Forêt Antsahabe, 11.4 km 275° W Dairana, 550 m (Fisher, B. L.; et al.); Forêt Binara, 9.1 km 233° SW Dairana, 650–800 m (Fisher, B. L.; et al.); P.N. Marojejy, 27.6 km 35° NE Andapa, 775 m (Fisher, B. L.; et al.); R.S. Manongarivo, 10.8 km 229° SW Antanambao, 400 m (Fisher, B. L.); R.S. Manongarivo, 12.8 km 228° SW Antanambao, 780 m (Fisher, B. L.); *Fianarantsoa*: 43 km S Ambalavao, Res. Andringitra, 800 m (Fisher, B. L.); 43 km S Ambalavao, Res. Andringitra, 825 m (Fisher, B. L.); 45 km S Ambalavao, 785 m (Fisher, B. L.); Ambodiamontana [as "Ambodiamatana"], Ranomafana Natl Pk, 800 m (Rajeriarison, E.); Miaranony, Ranomafana Natl Pk, 1050 m (Rajeriarison, E.); Miaranony, Ranomafana Natl Pk, 700 m (Rajeriarison, E.); Nat. Park Ranomafana, Miaranony, 1050 m (Rajeriarison, E.); P.N. Ranomafana, 1130 m (Harin'Hala, R.); P.N. Ranomafana, Vatoharanana, 4.1 km 231° SW Ranomafana, 1100 m (Fisher, B. L.; et al.); PN Befotaka-Midongy, 940 m (Fisher, B. L.; et al.); R.S. Ivohibe, 8.0 km E Ivohibe, 1200 m (Fisher, B. L.); R.S. Ivohibe, 9.0 km NE Ivohibe, 900 m (Fisher, B. L.); Ranomafana Natl Pk. (Rajeriarison, E.); Ranomafana, Miaranony Village (Kingman, A.); Valoloaka Forest, Ranomafana Natl Pk, 1150 m (Rajeriarison, E.); Vevembe, 600 m (Fisher, B. L.; et al.); *Toamasina*: 17 km W Andapa, Res. d'Anjanaharibe-Sud, 875 m (Alpert, G. D.); 1 km SSW Andasibe (=Périnet), 920 m (Ward, P. S.); 6.5 km SSW Befingotra, Res. Anjanaharibe-

Sud, 875 m (Fisher, B. L.); 9.2 km WSW Befingotra, Res. Anjanaharibe-Sud, 1280 m (Fisher, B. L.); Andasibe (Périnet) (Brooks, R. W.); Betampona, 390 m (Fisher, B. L.; et al.); Betampona, 520 m (Fisher, B. L.; et al.); F.C. Andriantately, 530 m (Ratsirarson, H. J.); F.C. Sandranantitra, 450 m (Ratsirarson, H. J.); Forêt Ambatovy, 14.3 km 57° [NE] Moramanga, 1075 m (Fisher, B. L.; et al.); Forêt Analamay, 19.1 km 51° NE Moramanga, 1068 m (Fisher, B. L.; et al.); Forêt Torotorofotsy, 14.9 km 71° ENE Moramanga, 1070 m (Fisher, B. L.; et al.); Manakambahiny (Pauly, A.); Mont. Anjanaharibe, 18.0 km 21° NNE Ambinanitelo, 470 m (Fisher, B. L.; et al.); Mont. Anjanaharibe, 19.5 km 27° NNE Ambinanitelo, 1100 m (Fisher, B. L.; et al.); P.N. Mantadia, 895 m (Ratsirarson, H. J.); PN Zahamena, 860 m (Fisher, B. L.; et al.); PN Zahamena, Besaky River, 760 m (Fisher, B. L.; et al.); PN Zahamena, Oribe River, 780 m (Fisher, B. L.; et al.); PN Zahamena, Sahavorondrano River, 765 m (Fisher, B. L.; et al.); vic. Andasibé (=Périnet), 950–980 m (Brown, W. L.; Brown, D. E.); *Toliara*: 10 km NW Enakara, Rés. Andohahela, 420 m (Fisher, B. L.); Env. de Tsivory (Région du Sud) (Vacher); Forêt Ivohibe, 200 m (Fisher, B. L.; et al.); Forêt Ivohibe, 650 m (Fisher, B. L.; et al.); Fort Dauphin (Sikora); Grand Lavasoa, 450 m (Fisher, B. L.; et al.); P.N. Andohahela, Manampanihy, 5.4 km 113° ESE Mahamavo, 650 m (Fisher, B. L.; et al.); PN Andohahela, 275 m (Fisher, B. L.; et al.); *province unknown*: "Madagascar Central" (Sikora); "Madagascar/(S.-E.)" (Decary, R.).

Worker measurements (n = 9). HW 1.16–1.59, HL 1.23–1.74, LHT 1.38–1.83, CI 0.90–0.94, FCI 0.11–0.15, REL 0.31–0.34, REL2 0.34–0.38, SI 0.76–0.82, FI 0.28–0.32, PLI 0.49–0.56, PWI 0.46–0.53.

Worker diagnosis. Similar to *T. grandidieri* (q.v.). Basal margin of mandible with conspicuous tooth (Fig. 1); anterior clypeal margin deflected ventrally; head relatively broad (CI 0.90–0.94); metanotal spiracle visible in lateral view of mesosoma; dorsal face of propodeum broadly convex in posterior view; standing pilosity and appressed pubescence generally sparse; integument mostly sublucid, with fine coriarius/puncticulate sculpture; orange to

reddish-brown, appendages paler; head usually concolorous with mesosoma.

Comments. This is one of the more distinctive species in the *T. grandidieri* group, easily recognized by the presence of a tooth on the basal margin of the mandible and by the undercut median portion of the clypeus. *T. merita* is usually more or less unicolorous reddish- or orange-brown, without a contrastingly darker head, but in some northern populations (3.9 km S Ambaliha, Forêt Antsahabe and Forêt Binara) the head is infuscated relative to the rest of the body. This species also tends to be larger than all the others except *T. manangotra* (see HW, HL and LHT measurements). Although the holotype of *T. grandidieri hildebrandti* (Forel, 1891) is conspecific with *T. grandidieri* (Forel, 1891), material referred to *T. g. hildebrandti* by Forel (1892: 260) includes *T. merita*. During earlier examination and identification of museum material I assigned the code name *Tetraponera* psw92 to this species.

Distribution and biology. *T. merita* is widely distributed in rainforest of eastern and northern Madagascar, overlapping the ranges of all other species in the *T. grandidieri* group (Fig. 26). Nests have been found on the ground in rotten logs, sticks and tree stumps. A worker from the type series (PSW10943) stung me on my left index finger. The sting was rather painful and left a pustule that lasted more than a week. It reinforced my impression that the conspicuous orange and reddish-brown coloration of workers of *T. merita* and related species in the *T. grandidieri* group is aposematic.

***Tetraponera variegata* (Forel 1895) stat. n.**
(Figs 21–22, 24)

Sima Grandidieri var. *variegata* Forel 1895: 487. Syntypes, 2 workers, "Centr Madag." (Sikora) (MHNG) [examined] [Imaged on AntWeb: CASENT0101045, CASENT0101046]. **Syn. n.** One syntype (CASENT0101046) here designated **lectotype**.

Tetraponera grandidieri var. *variegata* (Forel); Wheeler 1922: 1014. Combination in *Tetraponera*.

Tetraponera grandidieri var. *variegata* (Forel); Santschi 1926: 27. Description of queen.

Material Examined.—(CASC, MHNG, NHMB, PSWC) MADAGASCAR *Antananarivo*: 3 km 41° NE Andranomay, 11.5 km 147° SSE Anjozorobe, 1300 m (Fisher, B. L.; et al.); *Antsiranana*: PN Marojejy, 488 m (Irwin, M. E.); *Fianarantsoa*: 7 km W Ranomafana, 1100 m (Steiner, W. E.); Ranomafana National Park, Talatakely, 850 m (Irwin, M. E.; Schlinger, E. I.); RS Kalambatritra, Ampanihy, 1269 m (Fisher, B. L.; et al.); *Toamasina*: Moramanga (Descarpentries); Morarano-Chrome (Pauly, A.); *Toliara*: Forêt Ivohibe, 650 m (Fisher, B. L.; et al.); *province unknown*: "Centr Madag." (Sikora).

Worker measurements (n = 6). HW 1.15–1.36, HL 1.36–1.62, LHT 1.39–1.59, CI 0.80–0.85, FCI 0.13–0.17, REL 0.29–0.32, REL2 0.35–0.38, SI 0.76–0.81, FI 0.30–0.32, PLI 0.49–0.55, PWI 0.41–0.46.

Worker diagnosis. Similar to *T. grandidieri* (q.v.), but larger on average. Basal margin of mandible lacking tooth; anterior clypeal margin broadly convex and crenulate, directed forward; metanotal spiracle visible in lateral view of mesosoma; dorsal face of propodeum broadly convex in posterior view; standing pilosity and appressed pubescence generally sparse; integument mostly sublucid, with fine coriarius/punctulate sculpture; mesosoma, petiole and postpetiole orange-brown, head and gaster a contrasting blackish brown, legs with a black band on the distal portions of the femora.

Comments. *T. variegata* can be distinguished from related species by the bicolored body and black banded legs (Fig. 22). *T. grandidieri* lacks black banding on the legs and, although the body is often bicolored, only the head is dark, not the head and gaster (as in *T. variegata*). Although such color differences might appear to be a weak basis for treating *T. variegata* as a species distinct from *T. grandidieri*, the two forms have been col-

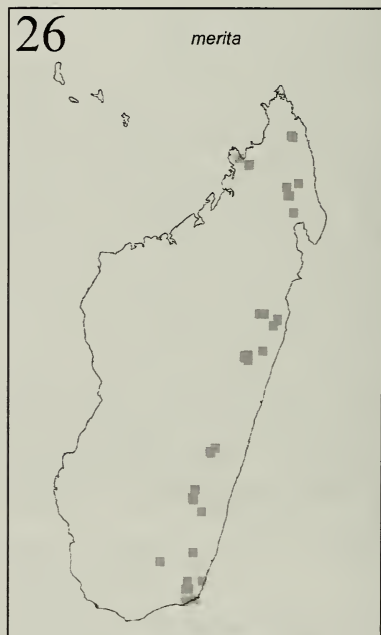
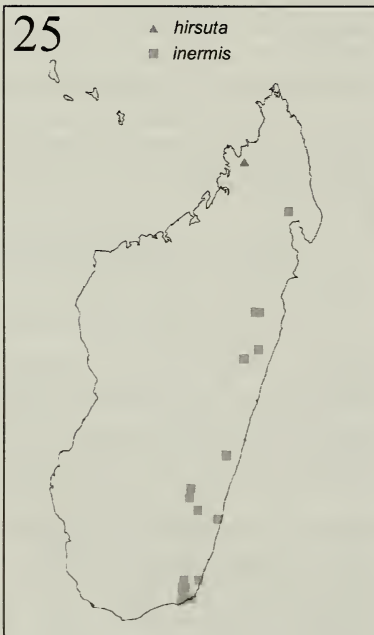
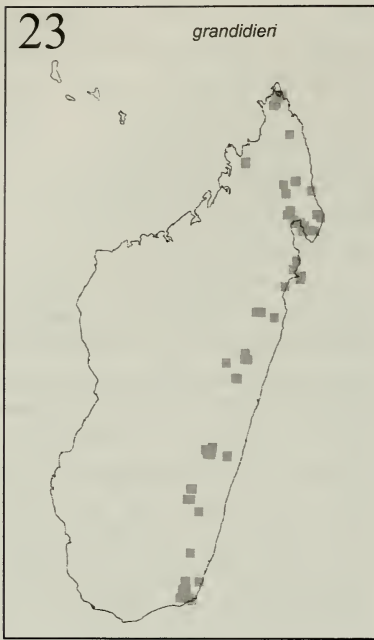
lected sympatrically at several sites (PN Marojejy, PN Ranomafana, Forêt Ivohibe) without showing any signs of intergradation. One other species, *T. hespera*, from northwestern Madagascar, exhibits black leg banding in most populations but in that species the body is unicolored light yellow or orange-brown.

I have designated a lectotype for *T. variegata* since there is a dealate queen in NHMB (Basel) from Moramanga (leg. Descarpentries) labeled, incorrectly, as a *variegata* "type". This specimen has no status as a type, but it reflects the practice of earlier myrmecologists of designating "type specimens" for queens and males when they were described later than the worker caste of the same species.

Distribution and biology. *T. variegata* is known from several widely scattered locations in the rainforest zone of eastern Madagascar (Fig. 24). Its range broadly overlaps the distributions of *T. grandidieri*, *T. inermis* and *T. merita*. Specimens have been collected in Malaise traps and foraging on vegetation. Up to this point no nests have been found.

CONCLUDING REMARKS

Workers of closely related ant species can often be distinguished by differences in pilosity, sculpture and shape. Yet the species in the *Tetraponera grandidieri* group show quite limited divergence with respect to these kinds of characters. A brief examination of the male genitalia of four species (*T. grandidieri*, *T. hespera*, *T. inermis* and *T. merita*) failed to yield any obvious differences in the shapes of the aedeagus, paramere or subgenital plate (abdominal sternite 9), even though male genitalia often provide useful differences among closely related species in other groups of pseudomyrmecine ants (Ward 1999, 2001). Nevertheless the species recognized here occur sympatrically in various combinations and the slight differences between them are not blurred where they co-occur. I



Figs 23–26. Distribution of the *Tetraponera grandidieri* group. 23, *T. grandidieri*; 24, *T. hespera* (squares), *T. variegata* (diamonds) and *T. manangotra* (triangle); 25, *T. hirsuta* (triangle) and *T. inermis* (squares); 26, *T. merita*.

conclude that although the taxa are likely to have diverged relatively recently they behave as good biological species. The ants have painful stings and their bright

orange-brown or reddish-brown colors appear to have an aposematic function—as is also indicated by the occurrence of non-stinging *Camponotus* ants whose work-

ers mimic those of the *T. grandidieri* group. It would be interesting to investigate the role of warning coloration and mimicry in maintaining species distinctness in this group.

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